Variability among Caribbean Littorinidae

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(4 Text figures)

THE DEFINITION OF a species is limited by the degree of variability which an author will accept. The literature of the Littorinidae includes more than 1000 references, over half of which include some taxonomic discussion.

The 3 species of the *Littorina ziczac* species complex, *Littorina lineata* d'Orbigny, 1841, *L. lineolata* d'Orbigny, 1840, and *L. ziczac* (Gmelin, 1791), as defined by BORKOWSKI & BORKOWSKI (1969) have been subjected to episodic subdivision and recombination since the time of Linnaeus. Recently, VERMEIJ & PORTER (1971) have suggested that a Brazilian subspecies, *L. ziczac brazilensis*, exists. BANDEL (1974) used the name *L. jamaicensis* C. B. Adams, 1850, for *L. lineata*, and suggested that certain populations from the coast of Colombia be considered a separate species within the complex. As will be shown below, however, shell, egg capsule, and radular characters purportedly distinguishing these groups, and used as grounds for splitting *Nodilittorina tuberculata* Menke, 1828 into 2 species, *N. tuberculata* and *N. dilatata* (d'Orbigny, 1841), are included within the normal range of variability of *L. lineata* and *N. tuberculata*, respectively.

The Shell: BEQUAERT (1943) emphasized that when a small sample of specimens is examined, it is relatively easy to distinguish varieties corresponding to most of the names in the synonymy of *Littorina ziczac s. l.*; but a large sample, even from one location, shows that these extremes are included within the range of variation. BORKOWSKI (1967) quantitatively determined the range of variation for a large number of shell characters for each of the 3 species in the *L. ziczac* species complex. BORKOWSKI & BORKOWSKI (1969) presented the results of correlation based upon these measurements in order to statistically validate their taxonomic separation of the 3 species.

No one shell character is adequate to separate the 3 species of the *Littorina ziczac* species complex, but for mature, second year animals (BORKOWSKI, 1974), the number, or number per millimeter, of spiral, incised lines on the body whorl usually separates *L. ziczac* from the other 2 species (Table 1). Shape, as characterized by spire or apical angle (Table 2) is usually sufficient to

Table 1

Comparison of the number of spiral incised lines on the body whorl among *Littorina lineata*, *L. lineolata*, and *L. ziczac*

Lines per mm	*Littorina lineata*	*Littorina lineolata*	*Littorina ziczac*
Number of animals:	367	372	57
1			
2	11%	65%	
3	68	34	
4	17	1	4%
5	4		38
6			31
7			13
8			10
9			4

Table 2

Comparison of spire angles among *Littorina lineata*, *L. lineolata*, and *L. ziczac*

Degrees	*Littorina lineata*	*Littorina lineolata*	*Littorina ziczac*
Number of animals:	405	164	51
45°	1%		10%
49	39		27
53	53	1%	37
57	7	17	22
61		54	4
65		26	
69		2	

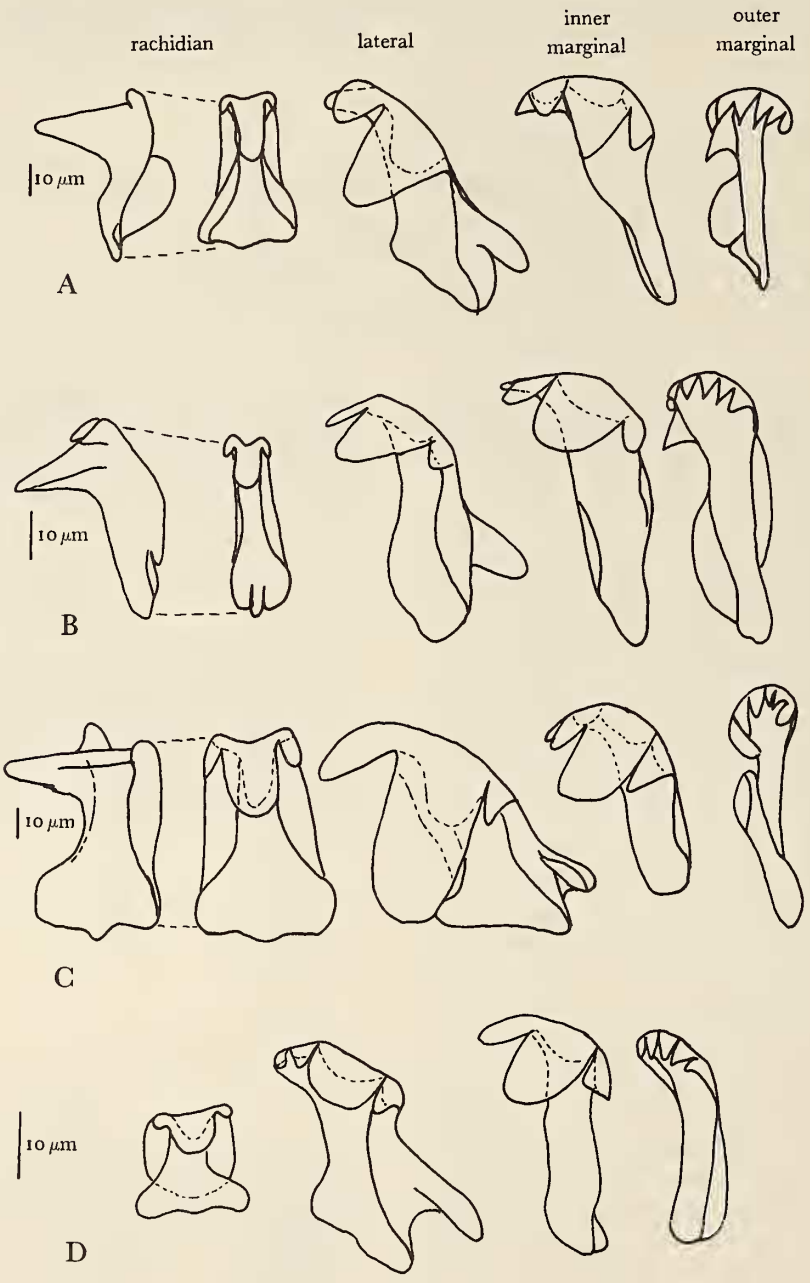

Figure 1

Half-rows of the radulae of 4 species of the genus *Littorina*:

A – *Littorina lineata* B – *L. lineolata* C – *L. ziczac*
D – *L. meleagris*
The line to the side of each radular row equals 10 μm

separate *L. lineata* from *L. lineolata*. In neither case is actual measurement necessary or called for. The presence of 1 spiral color band, or line, in the aperture will usually distinguish *L. lineolata*, but 5% of the specimens may have 2. Specimens of *L. ziczac* and *L. lineata* usually have 2 lines in the aperture, but 5% of *L. ziczac* specimens may have only 1, and 10% of *L. lineata* specimens may have 3, or 1, or be completely dark. Difficult specimens of *L. lineolata* also may be separated from *L. lineata* by tendencies for the flammulations on the body whorl of *L. lineolata* to be more zigzag and to subdivide near the shoulder of the shell. In all cases, separation is simplified by segregation and identification of shells in groups rather than as individual specimens. Bandel's *L.* sp. easily falls within the range of variation of *L. lineata*.

More difficult to identify are 1st year, smaller specimens. Borkowski (1970, 1974) showed that significant allometry, *i. e.*, change in shell shape with growth in size, occurs for *Littorina lineolata*, but not for 5 other littorinid species. *Littorina lineolata* appears quite similar to *L. lineata* in shape at sizes smaller than about 6mm in height; then an increasing spiral angle (see Fretter & Graham, 1962) results in an increasing apical angle and a squatter shape so that the species are easily separated.

Borkowski (1970, 1974) has also shown that variable success in the recruitment of young into a population of littorinids can dramatically alter the appearance of a population. With the influx of the 1968 year-groups into the *Littorina lineata* and *L. lineolata* populations at Government Cut, Miami, Florida, older, easily-identifiable animals were more rarely collected, and group rather than single-shell comparisons were necessary for reliable identification. Similar difficulties were experienced with specimens received or examined from the Florida Keys, the West Indies, Colombia, Mexico, and from Brazil. In each case, however, specimens of older, easily-identifiable shells confirmed preliminary identifications. Vermeij & Porter's *L. ziczac brazilensis* probably represents populations of 1st year *L. lineata*.

Bandel (1974) inappropriately used the name *Littorina jamaicensis* C. B. Adams, 1850, for *L. lineata* d'Orbigny, 1841. This name is clearly referable to *L. lineolata* d'Orbigny, 1840, according to the description and figures of C. B. Adams as reprinted by Mörch (1876) and Clench & Turner (1950).

Examination of a growth series of *Nodilittorina tuberculata*, and studies by Borkowski (1970, 1974) have shown that shell characters such as development of a callus in this and related species is related to a slowing of growth both at maturity and at the end of seasonal growth. Most large samples of *N. tuberculata* will show the extremes of nodule development used by Bandel (1974) to split *N. tuberculata* into 2 species.

Egg Capsules: Differences among published drawings of egg capsules from *Littorina lineata, L. lineolata, L. ziczac,* and *Nodilittorina tuberculata* by Bandel (1974), Borkowski (1971), Lebour (1945), Lewis (1960), and Marcus & Marcus (1963) suggest that ornamentation of the egg capsule in these species may be subject to considerable regional variation. Borkowski (1971) showed that considerable variation can also occur at one location and figured 2 apparently quite different capsules from the observed range of capsule ornamentation for *L. lineata* and *N. tuberculata*. These observations suggest that egg capsule ornamentation has not been adequately validated as a species-level taxonomic character.

Radular Characters: The taxonomic value of the radula at the species level has been questioned by several authors (Carriker, 1943; Howe, 1930; Merriman, 1967; Pruvot-Fol, 1926). These authors found considerable variation of radular tooth shape and number among individuals of the same species and very strong radular similarities between species. But Adam (1933, 1941) was able to show that so-called anomalies in the cusps of the rachidian tooth of octopods were serially repeated and of value for species discrimination. Olsson (personal communication) and Baker (1923) have suggested that the radula may be useful for species discrimination in *Olivella* and the Neritidae, respectively. Abbott (1954), Bandel (1974), Borkowski (1967), Marcus & Marcus (1963), and Whipple (1965) noted slight differences in cusp size and shape of littorinid radulae, but an assessment of variation was not made.

Accordingly, for 8 species of littorinids (*Littorina angulifera, L. lineata, L. lineolata, L. ziczac, L. meleagris. Nodilittorina tuberculata, Tectarius muricatus,* and *Echininus nodulosus*) a small part of the radular ribbon just anterior to the radular sac, *i. e.*, a part where the teeth are fully formed and free of wear, was removed from 5 specimens of similar size of each species. The ribbon was stained in aceto-carmine, dehydrated in an alcohol series, and mounted; several teeth were dissected from a broken end of the ribbon fragment with a sharpened dissecting needle and fine forceps before mounting. Teeth were drawn by camera lucida and measurements were taken with an ocular micrometer, accurate to 3 μm, of the height and width of each tooth and the lengths of each cusp of each tooth. The central cusp length of the rachidian included the basal part to which the cusp was at-

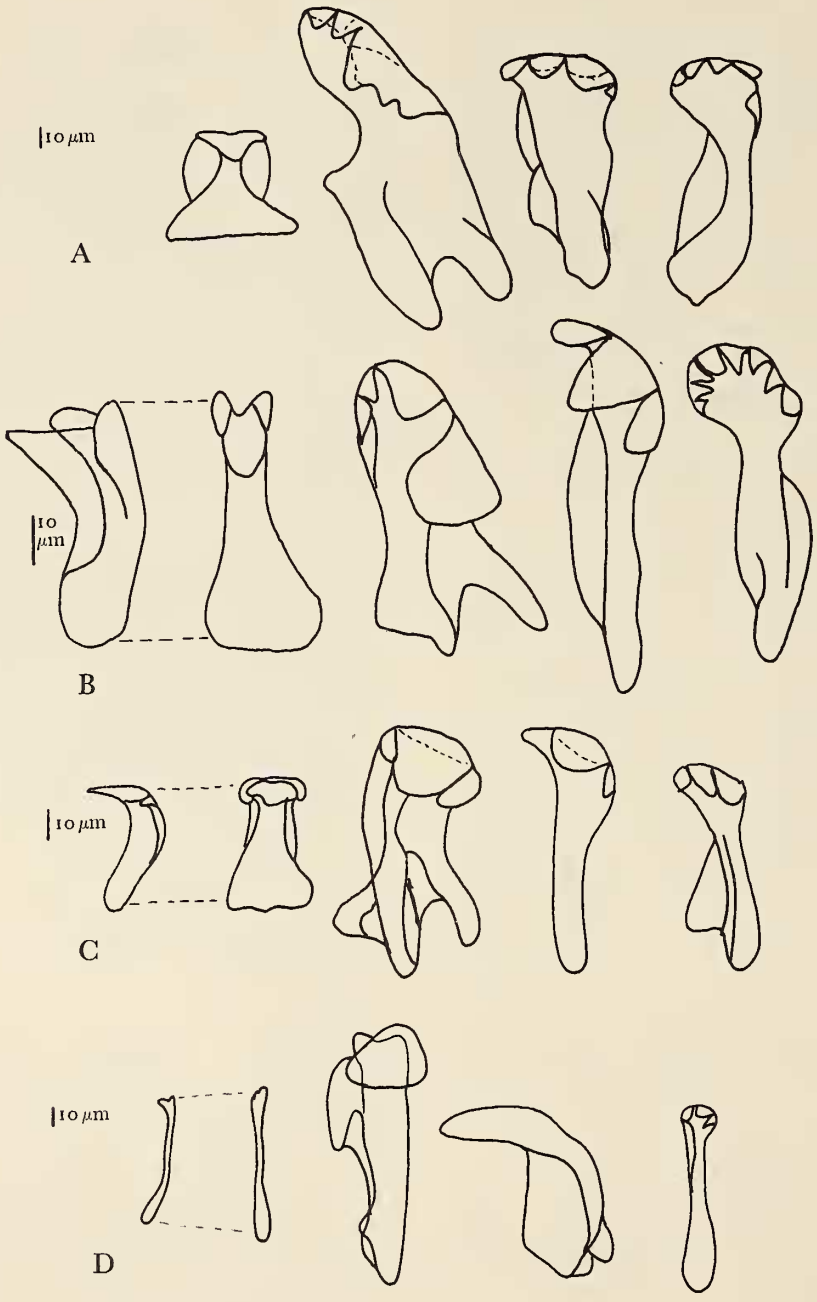

Figure 2

Half-rows of the radula of representatives of 4 littorinid genera:
A – *Littorina angulifera* B – *Nodilittorina tuberculata*
C – *Tectarius muricatus* D – *Echininus nodulosus*

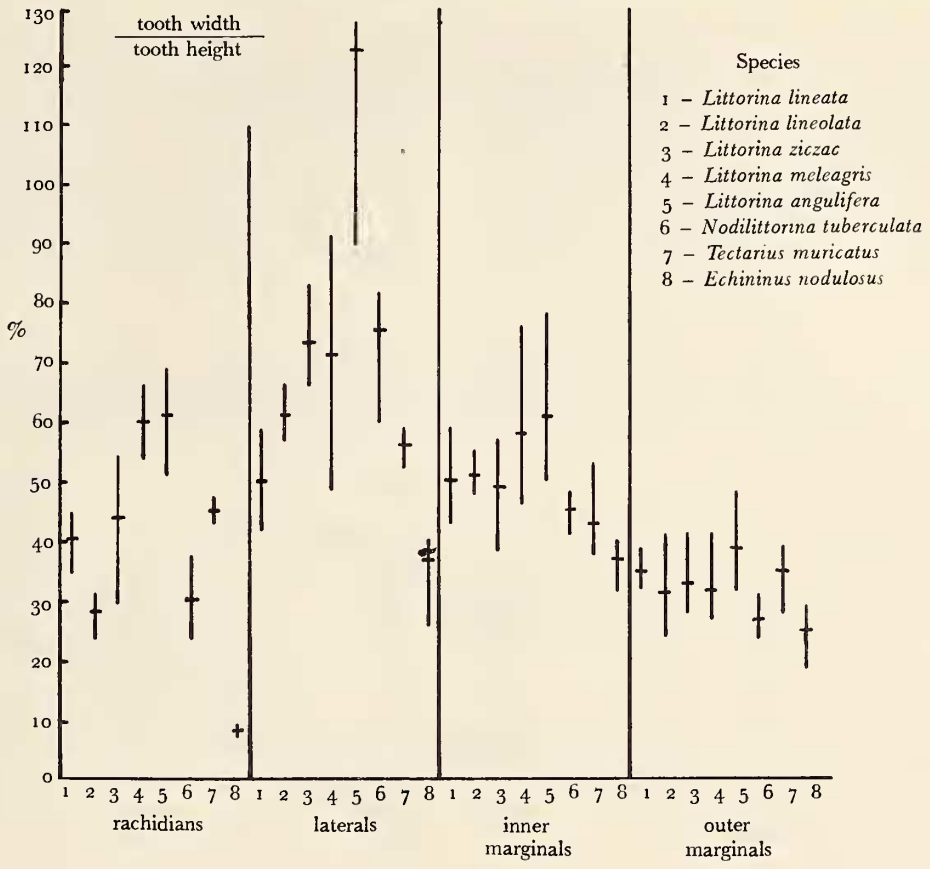

Figure 3

Comparisons of littorinid radular tooth-width : tooth-height indices

Table 3

Variation in the indices of the radula of *Littorina lineolata* as a result of size of the animal

	Shell ht. (mm)	Rachidian	Lateral	Inner Marginal	Outer Marginal
Index width/height	9.1	17	52	45	29
	7.2	21	60	42	28
	5.4	45	54	39	34
		(1 2 3)	(1 2 3)	(1 2 3)	(avg.)
Index cusp length/tooth height	9.1	8 44 8	26 67 7	17 62 8	10
	7.2	8 54 8	46 67 21	26 36 6	12
	5.4	10 76 10	25 42 6	33 40 6	8
Index tooth height/lateral height	9.1	86		90	90
	7.2	100		127	121
	5.4	60		100	71
Index tooth width/lateral width	9.1	21		78	41
	7.2	34		90	55
	5.4	50		74	74

Table 4

Cusp number and relative sizes of the radular teeth of eight species of tropical west Atlantic *Littorinidae*

	1[1]	2	3	4	5	6	7	8
RACHIDIAN								
Index & range								
wth/ht	40(10)[2]	28(7)	44(24)	60(12)	61(18)	30(13)	45(4)	8(2)
Cusp #	3	3	3	3	3	3	3	2
Index & range								
cusp 1/tooth ht								
central	72(44)	72(15)	55(22)	40(8)	40(15)	52(22)	44(19)	25(9)
lateral	24(14)	24(9)	13(6)	17(9)	12(15)	12(13)	14(8)	5(2)
LATERAL								
Index & range								
wth/ht	50(17)	61(9)	73(17)	71(42)	105(37)	75(22)	56(7)	37(14)
Cusp #	3	3	3	4	5	3	3	2
Index & range								
cusp 1/tooth ht								
1 (medial)				10(6)	10(8)			
2	40(35)	36(18)	38(19)	18(21)	11(11)	32(44)	12(8)	
3	61(45)	57(22)	75(50)	41(26)	23(54)	67(31)	56(22)	64(9)
4	17(17)	13(12)	15(13)	15(24)	10(16)	12(9)	12(7)	3(2)
5					8(6)			
side projection	yes	yes	yes	yes	yes	yes	yes	yes
INNER MARGINAL								
Index & range								
wth/ht	50(16)	51(7)	49(18)	58(30)	61(28)	45(7)	43(15)	37(8)
Cusp #	4	3	4	3	4	3	3	1
Projection	no	no	no	no	no	no	no	no
Index & range								
cusp 1/tooth ht								
1	12(10)				13(8)			
2	25(13)	27(14)	22(19)	19(15)	17(11)	18(11)	20(12)	
3	37(13)	50(16)	38(22)	40(32)	17(18)	37(12)	36(13)	76(15)
4	21(8)	21(11)	20(6)	13(5)	6(3)	11(5)	11(10)	
5			8(4)					
OUTER MARGINAL								
Index & range								
wth/ht	35(6)	31(17)	33(13)	32(17)	39(16)	27(7)	35(11)	25(10)
Cusp #	6-7	6-7	5-6	5-6	4-5	6-7	3-4	3-4
Side projection	yes	yes	yes	no	yes	yes	yes	no
Index & range								
cusp 1/tooth ht								
average only	10(6)	8(3)	16(10)	13(11)	12(11)	12(7)	15(8)	10(2)
Index & range								
tooth ht/lateral ht								
rachidian	63(15)	66(39)	87(53)	87(52)	93(33)	86(21)	79(12)	52(13)
inner marginal	100(28)	99(34)	142(61)	126(48)	146(85)	120(31)	137(28)	73(10)
outer marginal	90(22)	99(32)	141(71)	130(92)	181(65)	134(24)	129(47)	65(21)
Index & range								
tooth wth/lateral wth								
rachidan	52(21)	32(19)	52(10)	73(20)	54(20)	35(6)	63	13(5)
inner marginal	99(49)	82(25)	96(54)	104(33)	83(25)	76(22)	105(61)	87(27)
outer marginal	63(17)	53(31)	63(42)	59(23)	66(24)	50(13)	79(32)	52(18)

[1]1 = *Littorina lineata*, 2 = *L. lineolata*, 3 = *L. ziczac*, 4 = *L. meleagris*, 5 = *L. angulifera*, 6 = *Nodilittorina tuberculata*, 7 = *Tectarius muricatus*, 8 = *Echininus nodulosus*

[2]mean value (range in parentheses)

tached. Tooth measurements were combined in several ways to form indices, and indices and patterns of indices were compared. An additional series of 3 specimens of *L. lineolata* was measured to determine the effects of size of the animal on index values.

Comparisons among drawings by Abbott (1954), Bandel (1974), Marcus & Marcus (1963), and Figures 1 and 2 suggest that littorinid radulae show both intraspecific regional variation in radular tooth shape and in the number and shape of cusps on each tooth, and, at the same time, interspecific similarities. Significant changes in the shape of individual teeth may occur as the animal increases in size (Table 3), changes which differ in extent (Table 4). Index patterns (Figure 3) possibly could be developed as useful taxonomic characters, but direct interspecific comparisons of radular tooth shape and cusp

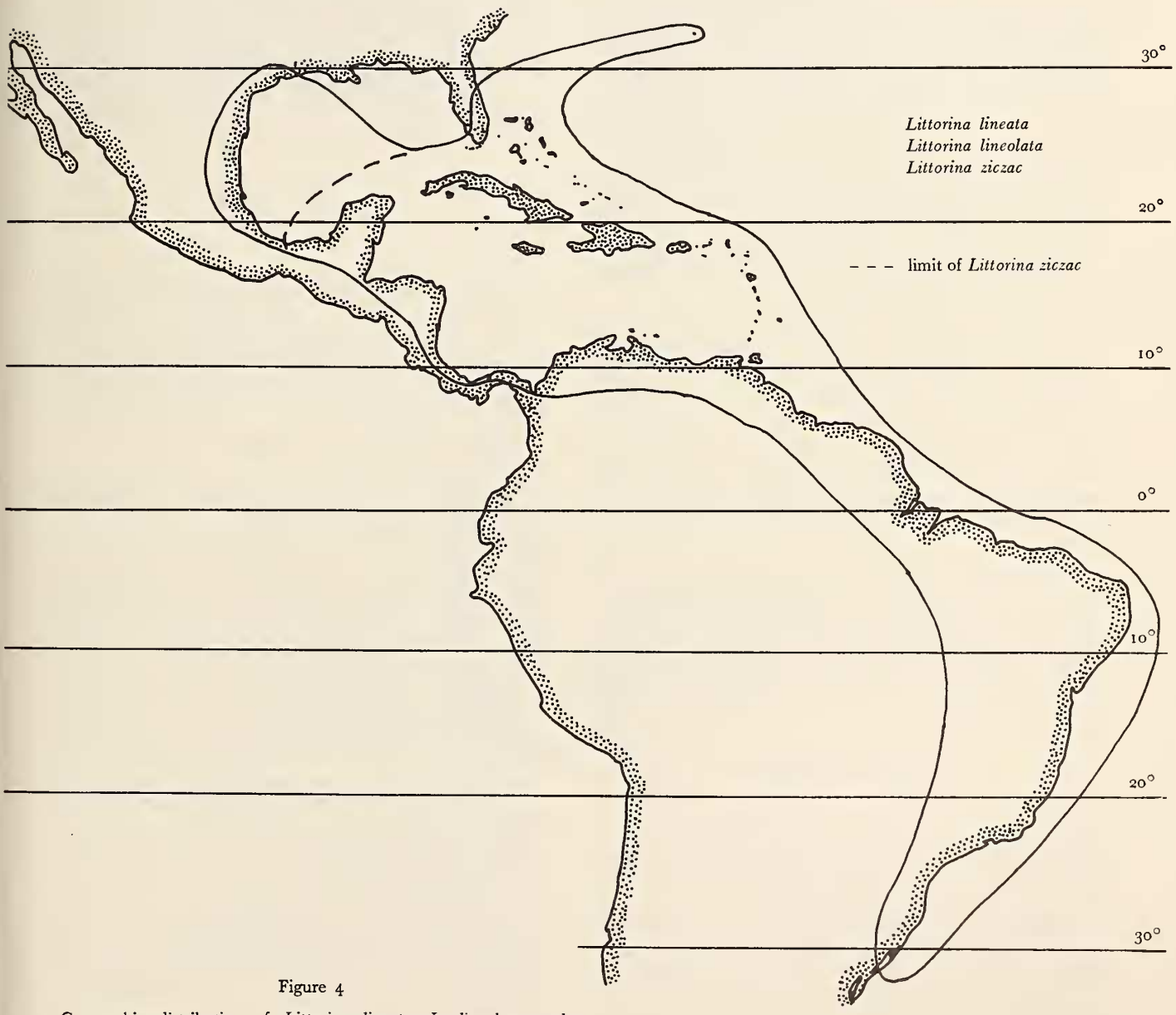

Figure 4

Geographic distribution of *Littorina lineata, L. lineolata,* and *L. ziczac*

number do not appear to have been sufficiently validated by studies of intraspecific variation. Differences in cusp number and shape observed by BANDEL (1974) could not have been due entirely to differences in methods.

Distribution: The distribution of the *Littorina ziczac* species complex is shown in Figure 4, as compiled from literature references, from the examination of specimens in a number of public and private collections, and from specimens donated by collectors located throughout the range of the species. A complete listing of sources and species localities is available upon request from the author. *Littorina lineata* has been collected rarely in Texas. Two specimens of *L. ziczac* were collected in beach drift at Galveston, Texas, following a hurricane, but no specimens were found in live-animal collections from various locations in Texas. BINGHAM (1973) reported occasional specimens of *L. lineolata* on the jetty at Panama City, Florida, but no established population. The Panama City jetty, however, is unusual in that, inexplicably, the occurrence of "tropical" species from several phylogenetic groups has been reported whose nearest known population may be several hundred kilometers away.

The distribution of *Nodilittorina tuberculata, Echininus nodulosus*, and *Tectarius muricatus* follows that reported by ABBOTT (1954) with the following range extensions. MATTHEWS (1968) reported on literature references to and specimens of *N. tuberculata helenae* Mellis in Smith, 1890, from Ilha Fernando de Noronha off the coast of Brazil. JAUME (1946) found *N. tuberculata* on the Yucatan Peninsula; specimens collected by Dr. Julia Hubbard in May, 1970, on Isla Mujeres confirm its presence in the area.

Bermuda specimens of *Echininus nodulosus* were found in the Simpson Collection at the Rosenstiel Institute of Marine and Atmospheric Sciences, Coral Gables, Florida. KRISTENSEN (1965) reported its presence on Aruba, Klein Curaçao, and St. Martin, Netherlands Antilles. Yucatan specimens of *Tectarius muricatus* were reported by JAUME (1946).

CONCLUSIONS

Both *Littorina lineata* and *L. lineolata* are found in Brazil. Populations of small littorinids called *L. ziczac brazilensis* by VERMEIJ & PORTER (1971) probably represent 1st year or early 2nd year *L. lineata*.

Similarly, both *Littorina lineata* and *L. lineolata* are found in Colombia. Shell variation in *L. lineata* easily includes the distinguishing characteristics of *L.* sp. as described by BANDEL (1974). Substitution of the name *L. jamaicensis* C. B. Adams for *L. lineata* appears to be inappropriate. Characteristics used to split *Nodilittorina tuberculata* into 2 species represent extremes of variation of *N. tuberculata*.

Allometric changes in shell shape and fluctuations in the success of recruitment of young into *Littorina lineata* and *L. lineolata* populations can cause considerable difficulties in the identification of small specimens of either species. Regional and intrapopulation variation in ornamentation of littorinid pelagic egg capsules, and intraspecific variation and interspecific similarities in radular tooth shape and the number and shape of the cusps on each tooth, suggest that both egg capsule ornamentation and radular characters require further validation as taxonomic criteria.

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